whitish; wings pale, whitish in parts, with the marginal bands and spots on fore wings visible.

Expanse of wings $\frac{9}{10}$–1 inch.

Cherra Punji. Two examples.

Much resembling *Nymphula irisalis*, Walker, from Sierra Leone.

Genus Cymoriza, Guen.

45. *Cymoriza albicomma*, sp. n.

♂. Reddish ochreous, suffused in parts with brownish. Wings with a small white spot ringed with black at the end of each cell: fore wings with a white comma-like mark from costa one third from base; a short white band from costa one fifth from apex to the middle of the wing; a short thin white streak inwards from this band near and parallel to the costa; another similar streak lower down, which runs into the cell-spot; a submarginal white line, which curves inwards above the hinder margin and is here thicker, also a fine marginal white line; all these white lines, bands, and streaks are bordered on each side with black, the black line on the inner side of the marginal white line being composed of black lunules: the hind wing has the white band from the costa near the apex and the submarginal and marginal lines similar to those on the fore wings, except that the submarginal line stops before reaching the anal angle.

Expanse of wings $\frac{8}{10}$ inch.

Shillong. One example.

The fore wings are marked somewhat like *Ambia locuples*, Butler.

XXX.—*Development of the Lungs of Spiders.*

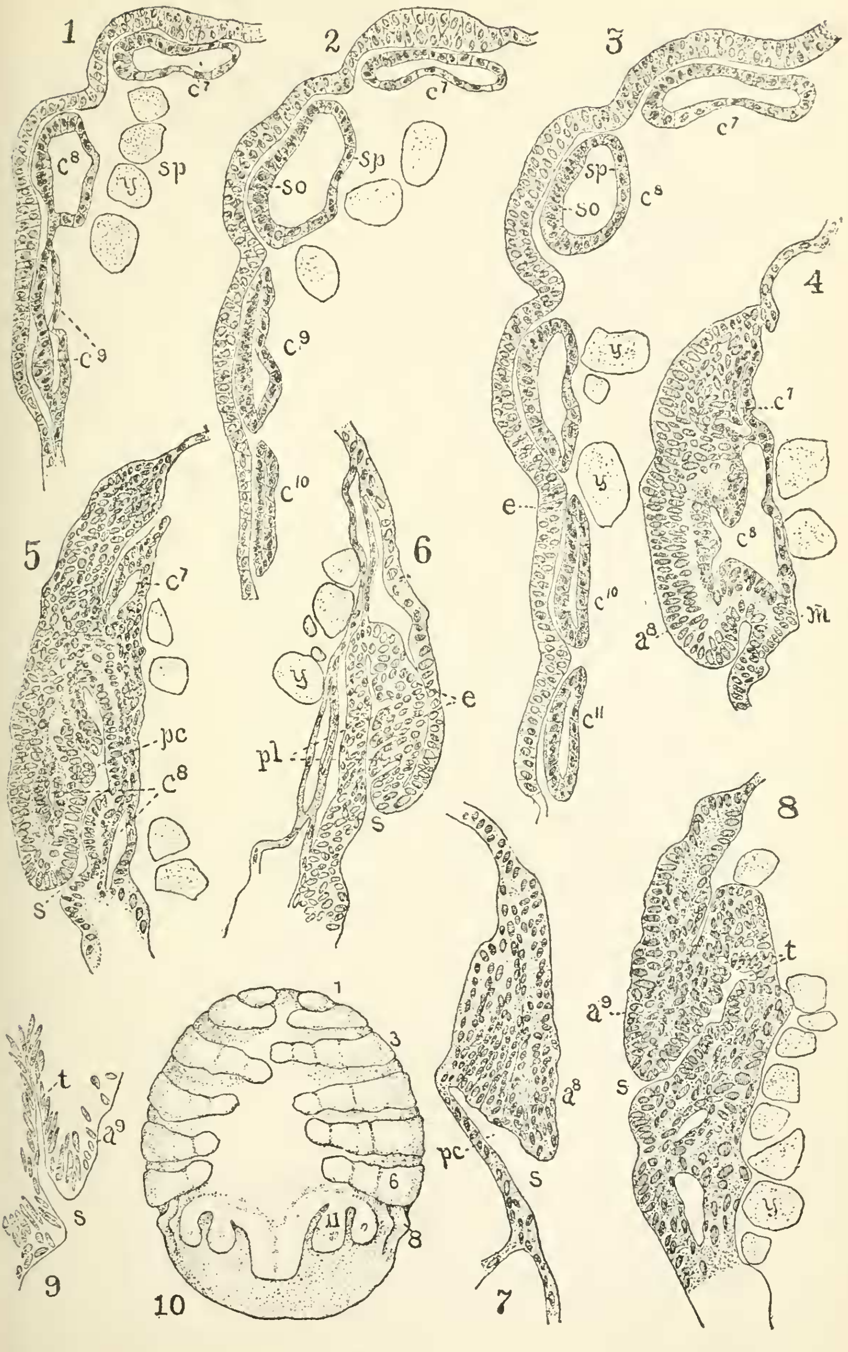
By Orville L. Simmons *.

[Plate VI.]

Although several persons † had suggested the close affinity of the Arachnids and *Limulus*, it was not until the appearance of Lankester's paper "*Limulus* an Arachnid" (1881[b]) that the view of such a relationship came into prominence. Since that date it has attracted more and more numerous advocates, until now the majority of the special students of

* From the 'American Journal of Science,' August 1894, pp. 119–128.

† Straus-Durckheim (teste Lankester), van Beneden (1870).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Arachnids and Xiphosures recognize the close relationships of the two groups. One of the special homologies insisted upon by Lankester was that existing between the lungs of the Arachnids and the gills of *Limulus*. But to explain the differences between these organs—the one being an internal air-breathing structure, the other an external apparatus for aquatic respiration—several hypotheses have been advanced, all based upon conditions existing in the adult.

At first Lankester evidently shared the common view that tracheæ were homologous structures throughout the Arthropoda, and so he sought for traces of them in *Limulus*. In his article "On Stigmata in the King-Crab" (1881[a]) he announced that he had found traces of stigmata. The position of insertion of each thoracico-abdominal muscle is marked by a deep funnel-like depression of the integument, which from the external surface appears as a stigma.

Later, in his paper "*Limulus* an Arachnid" (1881[b]) he formulates an hypothesis to show how the gills of *Limulus* and the lungs of *Scorpio* (taken because more primitive than Spiders) could have been derived from a common ancestor, which he describes as being an aquatic form, breathing by book-like gills. To derive *Limulus* from such a form would involve only a few changes in dimensions and other unimportant points. To obtain the condition occurring in *Scorpio* he assumes that the cup-like depressions behind the appendages, as seen in *Thelyphonus*, became deeper and larger, finally engulfing the whole appendage. The walls then gradually extended over the cavity, leaving only a slit for communication with the exterior. As change of habits went on this slit was closed up, and another slit, still within the area formed by the closure of the primitive opening of the cave of invagination, was formed. Air would enter by this slit, where in *Limulus* and the early Scorpion ancestors there was blood-space. Thus a blood-space has been changed to an air-space. In the same way an air-space (that of the investing sac) has been converted into a blood-space. The atrophy of the muscles which move the gills in *Limulus* and similar forms was considered very essential to this theory. The difficulties involved in the changes of blood- and air-spaces were so considerable as to prevent the acceptance of this hypothesis.

Later Lankester (1885) put forth a new theory. Because of discoveries concerning the muscles (veno pericardiac) of *Scorpio*, as well as on account of the insuperable difficulties of his previous view, he gave up his old and advanced a new hypothesis. In the latter the common ancestor is assumed to have had six pairs of mesosomatic appendages, of which five were lamelligerous. These latter in *Scorpio* became smaller and served only for respiratory organs, soon becoming air-breathing. The four hinder pairs took a "trick" of growth, viz. an invagination of the appendages, beginning at their distal ends, so that they grew into the scorpion's body, turning their outside in, just as a glove may be turned wrongside out, beginning at the ends of the fingers. Thus the appendages would be tucked into the blood-sinus instead of growing out normally. The blood-sinus would become a venous sac around the appendage. He explains the "trick" of growth by the least-resistance theory—the pressure being exerted on the embryo before it leaves the mother.

J. MacLeod (1882 and 1884) sets forth an hypothesis by which he develops Scorpions and similar forms from a *Limulus*-like ancestor. His first proposition is that the abdomen of *Limulus* be considerably elongated without other change. This would cause the imbrication of the members to cease—each appendage would stand out by itself although closely following each other. Then suppose that the sternal plate increase in size and unite with the ventral surface of the abdomen. Thus the gill-book cavity would be entirely filled up by the sternal plate except in those cavities on the ventral side which contain the gills or lungs, now greatly reduced in size. In this condition the lungs are quadrangular plates, attached by two edges only. Inserted on each plate is a number of lamellæ which are attached by one side only. In this condition when removed from the water the lamellæ would cling together and be imperfectly in contact with the air. To be of service the lamellæ would have to unite their lateral edges to the plate, leaving only the posterior edge free. Thus MacLeod developed the lamellæ and other structures of the lungs of Arachnida. By a comparison of structures in the adult form MacLeod came to the conclusion that the tracheæ of Spiders are developed from the lungs.

J. S. Kingsley (1885 and 1893) advances a much simpler explanation to account for the transition from a *Limulus* gill-book to the lung-book of a spider or scorpion. By a sinking-in of the whole appendage bearing the gill-leaves and an increase of the inpushings of the integument and a decrease in the outgrowths the whole matter is explained. This involves a diminution of growth on the anterior side of the appendage and an increase of growth on the posterior side. These conditions would carry the appendage within the body-wall, where it would be situated as seen in the adult—the spiracle at the posterior end of the lung-cavity and the lamellæ projecting toward the posterior end of the body. As Kingsley states, viewed from a histological standpoint, the description of the pulmonary organ of the spider or scorpion applies, almost word for word, to the gill-book of *Limulus*. He believes that the lungs of spiders are the primitive and the tracheæ the derived structures. The tracheæ of the Hexapoda have no relation to the tracheæ of spiders, having an entirely different origin.

Malcolm Laurie (1890), in his article on "The Embryology of a Scorpion," thinks the lung-books are undoubtedly comparable to the abdominal appendages of *Limulus*, but hesitates to decide which of two propositions he advances is the correct one. He inclines towards the view that the lung-books of Scorpions are invaginated, *i. e.* the edge of each lamella in the *Limulus* gill-book corresponds to the interior fold between the lamellæ in the Scorpion lung-book. He imagines that he sees difficulties in explaining his second proposition, which states that the whole appendage has sunk without invagination into a cavity in the abdominal surface. By either proposition the air-space of the primitive condition would be air-space in the derived condition.

On the other hand, many comparative anatomists, recognizing the homologies pointed out years ago by Leuckart as existing between the lungs and tracheæ of spiders, and believing that these last were the homologues of the structures known by the same name in the Hexapods, have failed to recognize the cogency of the reasoning of the advocates of the Arachnidan affinities of *Limulus*. Thus Arnold Lang, in his 'Lehrbuch der vergleichenden Anatomie' (ii. Heft, p. 548, 1890), writes that the respiratory organs of Arachnoidea are tracheæ—tubular and book-like tracheæ. His view of the morphological signification of the latter is that they are modified tracheal tufts which, standing close together, have been flattened into hollow plates. He believes that the view of those who would bring the gill-books of *Limulus* and the lung-books of Scorpions and similar types into close relationship is artificial and unsupported by comparative anatomy and ontogeny.

So, too, Bernard (1892), in 'The Apodidæ,' says it is easiest to believe that the lung-books of the various forms are only a specially concentrated arrangement of tracheal tubes. He regards the tracheæ, including the lungs of all "Tracheates," as having their origin in dermal glands which have gradually been modified for respiratory purposes. He also states that in considering the relationships of these various forms the limbs are of so little importance that one might almost be tempted to leave them out of account. In a later paper on the Chernetidæ Bernard (1893) repeats in substance his earlier views.

In a word, these authors, regarding the tracheal form of respiration as the primitive—a premise which the observations of Moseley on the tracheæ of *Peripatus* seemed to render valid—have looked upon the air-tubes of the Arachnids as the primitive and the lungs as the derivative condition.

The question thus brought into prominence can only be settled by tracing the development of the respiratory organs of the Arachnidâ. Several authors have touched upon this question. Thus Locy (1886) describes the later stages of *Agelena nævia* as follows:—The lungs arise as a pair of extensive invaginations. In sagittal sections they appear as oblong plates of cells with the nuclei in parallel rows. These nuclei are flattened on one side and convex on the other. The cells of two adjoining rows unite by the edges toward which the convex sides of the nuclei project, and thus a lamella is formed. Later the nuclei of adjoining cells fuse, forming protoplasmic pillars, between which are the blood-lacunæ. Around each lamella is a chitinous membrane—the ventral and the dorsal being continuous at the free (posterior) end of the lamella. The cells of the ventral wall become arranged into two distinct layers. A part of the development described takes place after the hatching of the egg.

A. T. Bruce (1886–87) says that a lung-book of a spider may be regarded as an involuted appendage or appendages. He noticed that the abdominal appendages become less conspicuous and that slight folds appear on their *anterior* faces. He did not observe all the stages, and, judging from his text and figures, it is very evident that he was confused in some of his interpretations. K. Kishinouye (1890) states that in the basal part of the first abdominal appendage there is an ectodermic invagination, not deep or large. The wall of this pocket which faces the distal end of the appendage is thicker and its cells become arrranged in parallel rows. Two of these rows, adhering to each other, produce a lamella. He confirms Locy's description of the later stages. On the second abdominal appendage is another ectodermic invagination—a deeply invaginated tube which remains in about the same state of development until after hatching. The appendage shortens, but is not invaginated. He believes it is very probable that the lungs were derived from the respiratory apparatus of some *Limulus*-like aquatic form. He thinks that tracheæ are modified lungs.

Laurie (1890), beginning with his stage K, describes the changes in the abdominal segments of the Scorpion. At this stage the pectinæ and lung-book appendages are about equal in size and structure. In stage L the pectines have become folded in a direction transverse to their axes. The other appendages are pushed in, forming little cavities (directed forward) on the posterior sides of the appendages. In the stage M the pectines are separated from the body-wall at their distal ends. The lung-book inpushings are deeper and the cavities are divided up by lamellæ. In the last stage described (just before hatching) the pectines and lung-books have much the same structure as in the adult.

Morin (1888)* states that the lungs of the dipneumonous spiders arise in form of infoldings at the bases of the two appendages of the second abdominal segment. At the anterior end of the sac on the dorsal side is an infolding, which is the beginning of the lung-leaves. The space between two leaves connects directly with the body-cavity. Two adjoining leaves unite by the fusing of cells, as described by Locy. He agrees with Locy as to the later stages. Morphologically the lungs of Arachnida show great resemblance to the gills of *Limulus* and similar forms. He emphasizes the position of the infoldings on the posterior side of the appendage in both cases. The lungs of spiders are merely sunken gill-books of *Limulus*. As the appendage sinks the stigma is left as an opening between the posterior wall of the appendage and the body-wall. This author agrees with those who believe that tracheæ are modified lungs.

It must not be forgotten that Elias Metschnikoff (1870) described some features of the lungs of the Scorpions; but it is not easy to understand either his text or his figures beyond the fact that he states that the lungs develop behind the abdominal limbs.

As will be seen from the foregoing summary, the development of the respiratory organs of the Arachnids has not been followed throughout, and the gaps in our knowledge are at just the most critical points. To supply these deficiencies the investigations described below were undertaken.

The work was done in the Biological Laboratory of Tufts College. The eggs used were those of *Agelena nævia* and *Theridium tepidariorum*. The eggs were killed in water heated to 80° C. and hardened in alcohol, beginning with 50 per cent. The staining was usually *in toto* with alum cochineal. The sections described, unless otherwise specified, are sagittal.

* As summarized by Korschelt and Heider (1892), pp. 604–607. I cannot refer to the original text.

In the first stage studied, corresponding in general to Locy's fig. 6, somite VII is cut off from somite VIII. Somites VIII and IX are still united (Pl. VI. fig. 1), and the unsegmented mesoderm extends further back. The ectoderm is a single layer deep, except a portion over somite VII (possibly the incipient foundation of an appendage) and between VIII and IX. The infolding of ectoderm shows the first differentiation of external segmentation.

In the next stage (fig. 2), which is about midway between Locy's figures 6 and 7, the second abdominal somite is differentiated, and to a less extent the line between somite IX and somite X, which has developed, is marked off. The ectoderm has become thickened from somite VII to somite IX. It is to be noticed that the cœlomic pouches are flattened in all except somite VIII.

The succeeding stage (fig. 3) shows the same features carried still further. The XI somite has appeared. This stage corresponds to Locy's figure 7 or a stage a little earlier. I may note here that I have found at least as many cœlomic pouches as are described by Kishinouye in his "Note on the Cœlomic Cavity of the Spider," 1894.

After the stage just mentioned the appendages begin to be formed; no detailed account need be given of the external appearance of these, as in the main my observations are but the repetition of those of various authors, from Claparède to Kishinouye. They grow out, one on either side of somites VIII–X, as rounded knobs.

Pulmonary Organs.

In figure 4, which represents somites VII and VIII, the early appearance of the appendage is seen. In somite VII the cœlome is already greatly reduced, and no trace of an appendage is to be seen. In the next somite (VIII) the appendage is plainly visible. It is marked off from somite VII by a slight groove, while the groove separating it from somite IX is deeper and directed forward, giving the limb a markedly backward direction, a tendency which is even more pronounced in later stages. Its outer wall is formed of several layers of cells, while the cœlomic pouch sends into the budding appendage an outgrowth like that described by various authors.

With further growth the conditions just described become more strongly emphasized; the anterior demarcation of the appendage becomes more and more faint, while behind the inpushing becomes more and more marked, so that eventually a pit is formed, actually extending into the general body surface, the outer wall of the pit being formed by the appendage whose growth we are tracing. This pit forms the pulmonary sac and the opening of the inpushing persists as the respiratory stigma. At no time do the appendages rise to any considerable distance above the general abdominal surface.

The changes described can be seen by a glance at fig. 5, which, besides the points already mentioned, shows some other features worthy of notice. The cœlome of somite VII still persists; that of VIII has become divided into two portions, one of which remains in the appendage, while the other portion, reduced in size, has been pushed backwards by the ingrowing pulmonary sac. The sac itself is irregular in outline, its inner wall being slightly undulating, while its outer wall, *i. e.* the morphologically posterior surface of the appendage, has its ectoderm thrown into folds, the rudiments of the leaves of the lung-book. The ectoderm lining the inner wall of this sac is but a single cell in thickness, but that of the appendicular side is thicker, the nuclei being rather irregularly arranged, the pulmonary ingrowths forcing their way between them. In this stage but two lung-leaves are outlined, as shown in the figure.

In eggs of the same lot as the last a stage apparently a little older was found, and from it the section figured in 6 was drawn. In its general features the changes are slight, but there are some details of importance. From the fact that the plane of this section is not the same as that of the last, the appendicular cœlome is not shown, while the cœlomic cavity of the body is here much larger. So, too, the inner wall of the pulmonary cavity is shown to be thicker, a fact probably due to the obliquity of the section. In this stage four gill-leaves are shown, the most developed ones being the most distal ones. In these too the nuclei are already arranged with their major axes parallel to the plane of the leaves. Proximally the leaves are much shorter and the nuclei are irregularly arranged. These facts place it beyond a doubt that the growing-point of the organ is at the base of the appendage, a point of no little importance in comparison with the Xiphosures.

Figure 10 shows the ventral view of the embryo at the stage which figures 5, 6, and 8 represent in sections. This stage is about two or three days before the reversion of the embryo. Changes during this period are very rapid. In four to five days after this stage the lungs are almost fully developed and have about the same appearance as in hatched specimens, except in size and number of lamellæ. The embryo hatches in from seven to eight days after the stage figured in 10.

With the reversion of the embryo the changes rapidly proceed toward the adult condition. In fig. 7 I insert an illustration which serves to connect my account with the papers of Locy, Kishinouye, Laurie, and others. Here the gill-lamellæ have slightly increased in number while they have become greatly increased in length. In the figure the pulmonary sac is somewhat funnel-shaped, owing to a pulling open of the spiracle in some process of manipulation.

From this stage the transition to the conditions described by MacLeod and Locy is but slight; and although I have studied the later stages up to and even beyond hatching, my observations are but a confirmation of theirs, and so I do not repeat them here. The lungs are well developed and apparently ready to function as respiratory organs at the time of hatching. With the growth of the young spider the principal changes are an increase in the number of lamellæ and a corresponding increase in the size of the pulmonary organ, the new lamellæ being formed at the inner end of the sac.

Tracheæ.

The study of these has been a matter of considerable difficulty, and I have been able to follow with certainty only the earlier stages. The tracheæ arise behind the appendage on somite IX, which, in its earlier stages, has exactly the same history as appendage VIII. There is the same inpushing behind the limb, which results in its taking a position not pointing outward, but towards the median line and backward. In fig. 8 is seen the first differentiation of the tracheæ. The inpushing has given rise to the spiracle as before, but the sac which results does not show so markedly those infoldings of the appendicular wall which occur in the case of the lungs. There is at most but a slight undulation of this surface. At the inner end, however, two ingrowths are seen, the earliest indications of the formation of the tracheal twigs. It is, however, easy to see that these inpushings are to be compared with the infoldings which produce the lamellæ, while the undulations just referred to admit of the interpretation that they are aborted lung-leaves.

After the reversion of the embryo the same parts can be recognized (fig. 9). The inpushing has been carried to a greater extent, and sections in other planes show that this ingrowth is tubular in character. The cells lining its walls are elongate and are already taking the character shown in the tracheæ of the adult. At the inner end of the tracheal trunk thus formed the nuclei are arranged in a radiating or bush-like manner, apparently indicating that here is the place where the trunk is about to divide into the tracheal twigs; but I have not been able to trace any tracheal lumina between these cells. I have not followed the later history of the tracheal system with any detail, but think that the foregoing is sufficient to justify my thesis that the tracheæ and the lungs are to be regarded as homologous structures.

Conclusions.

From the preceding it will be seen that:—

I. The lungs of the spider arise as infoldings upon the posterior surface of the appendages of the second abdominal somite in the same manner as described by Kingsley (1885 and 1893) for the gills of *Limulus*. They have the same growing-point at the base of the appendage and form the lung-leaves in exactly the same way that the gill-leaves arise. In other words, the lung-book of the Spider (and presumably of all Arachnids which possess one) arises at first as an external structure upon the posterior surface of the abdominal appendages. These appendages sink in without any inversion or other complications, in exactly the manner theoretically deemed probable by Kingsley, so that there can no longer be any doubt as to the exact homology existing between the lungs of the spider and the first pair of gills in the horseshoe-crab.

II. The tracheæ develop from the next pair (third abdominal somite) of limbs. In their earlier stages these appendages show on their posterior surface a folding similar to that on the preceding members. From this it follows that the lung-book condition is the primitive, the tracheæ of the Arachnids being derived from it. And with these facts there is left no ground for those who regard the "Tracheata" as a natural group of the animal kingdom.

Tufts College, Mass.,
May 25, 1894.

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